A MUSCLE ATTACHMENT PROPOSAL FOR SEPTAL FUNCTION IN MESOZOIC AMMONITES

by R. A. HENDERSON

ABSTRACT. The unusual septal surface typical of lytoceratid ammonites is described from unique Western Australian specimens of the late Cretaceous Indopacific species *Pseudophyllites indra* (Forbes). Median dorsal septal recesses and inner septa combine to form a septate tunnel lying within the phragmocone; their free margins are complexly fluted like that of the septal periphery in contact with the outer shell wall. Functional analysis of the fluted septal recesses and inner septa suggest that they were not related to phragmocone strength but facilitated the attachment of adductor muscles. By analogy, a muscle attachment function is argued for the fluted septal periphery of *P. indra* and for the septal periphery of Mesozoic ammonites in general. The role of septal design in contributing necessary strength to phragmocone construction is re-evaluated and considered subordinate.

Muscle attachment translocation during growth, a special problem for ectocochleate cephalopods, was accomplished by the release of muscle attachment and rapid forward movement of the ammonite animal in its shell. Muscles were re-attached along a narrow zone at the free margin of a newly formed septum, convolution of which enlarged the attachment surface. It is argued that connecting rings of the siphuncle were preformed in the body chamber prior to movement of the animal; location of the siphuncle, details of its construction, and the nature of associated structures are consistent with this proposal. The muscle-attachment hypothesis is further supported by shell microfabrics known for Mesozoic ammonites, including new data for *Sciponoceras*. Gross differences in shell form and ornamentation which separate Mesozoic ammonites and nautiloids are thought to be due to differences in growth style, necessitated by the manner in which muscle attachments were translocated in members of the two groups.

AMMONITES were one of the most common shelled-invertebrate groups in Mesozoic seas and their shells, characterized by completely fluted septa and a ventral siphuncle, have attracted functional comment throughout the history of invertebrate palaeontology. Raup (1966, 1967) has demonstrated that the outer shell form of planispiral ammonites can be generalized to a mere three parameters. No such simplicity is apparent for septa which show a bewildering array of morphologies among Mesozoic members of the subclass yet are taxonomically specific, showing no more variation at the species level than any other test attribute. Clearly their morphology was under close genetic control, seemingly at considerable expense relative to the genetic investment in other elements of shell morphology. By implication the septa, or the body surface they replicated, must have fulfilled an important functional role for the living animal. Further, the clear phyletic changes of septal design shown by discrete lineages of Mesozoic ammonites (Wiedmann and Kullman 1981) suggest the constant operation of selection pressures tuning septal morphology to its functional role.

As reviewed by Westermann (1971) and Kennedy and Cobban (1976) a number of functions have been attributed to the fluting of ammonite septa since Owen (1843) suggested that they were designed in such a way as to impart necessary additional strength to the shell. Owen's view has been frequently endorsed in the literature (Zittel 1884; Pfaff 1911; Ruzhentsev 1946; Arkell 1949; Kennedy and Cobban 1976) and according to Westermann (1975) is the consensus of present-day opinion.

Maastrichtian specimens of *P. indra* (Forbes) from the Miria Marl, Carnarvon Basin, Western Australia show with exceptional clarity the extraordinary septal surface that typifies the Jurassic and Cretaceous suborder Lytoceratina. Its septal morphology is incompatible with the strength paradigm of function which is thereby brought into question. It is here re-evaluated for Mesozoic ammonites generally. An alternative proposal, that the complex morphology of the septal periphery was required for muscle attachment, is argued for *P. indra* and its general applicability to Mesozoic ammonites is examined.

Location of specimens. The following abbreviations are used to denote the repositories of figured specimens: WAM—Western Australian Museum, Perth; NMV—National Museum of Victoria, Melbourne; BM(NH)—British Museum (Natural History), London; OUM—Oxford University Museum, Oxford.

SEPTAL SURFACE OF *PSEUDOPHYLLITES INDRA*

Description

The periphery of the septal surface in contact with the outer shell is complexly fluted to the fourth order. Convex flutes, corresponding to saddles of the suture, widen towards the periphery and arch forward in an adapertural sense. Concave flutes, corresponding to lobes of the suture, arch backwards towards the shell apex and narrow towards the periphery so that they form conical vaults below the outer shell. Minor flutes die out rapidly away from the periphery and at approximately the mid-line between the periphery and centre of the septum, first-order flutes disappear. The septal surface is then essentially planar across a narrow zone which is horseshoe-shaped in plan view. Inside this zone the septal surface is curved uniformly backwards to form a pronounced depression, here termed the septal recess, occupying the mid-dorsal septal field (Pl. 48, figs. 2, 5; text-fig. 1). The
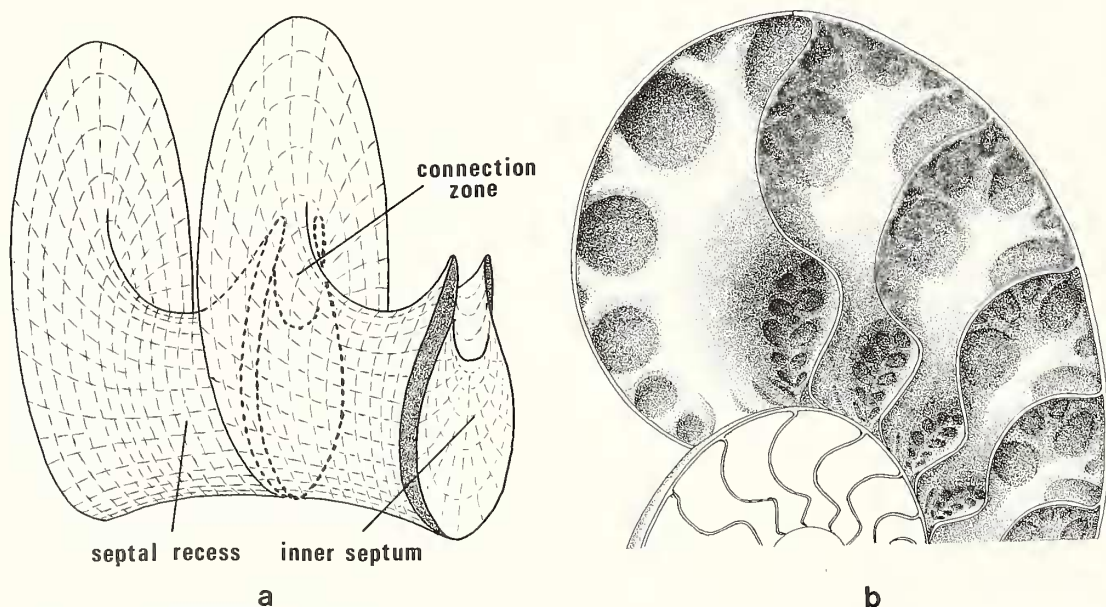
TEXT-FIG. 1. Septal architecture of *Pseudophyllites indra* (Forbes). *a*, schematic representation of two successive septal surfaces (fluting omitted). Note the zone of connection, provided by the neck of the inner septum, between each septal recess and the main chamber which succeeds it. *b*, phragmocone cut in the median plane; note the two chamber systems and the interconnection between them provided by the necks of the inner septa which do not close on to the preceding septal recesses.

EXPLANATION OF PLATE 48

Figs. 1–5. *Pseudophyllites indra* (Forbes) showing details of the septal surface. 1, 2, lateral and apertural view of phragmocone, WAM 60.44, ×1. 3, latex cast from internal mould of septal recess, WAM 81.2500, ×1. 4, latex cast from internal mould showing the fluted free margin of a septal recess and fluted inner septum. Note that the line of suture is continuous from the septal recess to the inner septum, both being part of a single septal surface, WAM 81.2433, ×4. 5, internal mould of septal surface showing septal recess and inner septum, WAM 60.130, ×1.

PLATE 48

1

2

3

4

5

HENDERSON, Septal function in ammonites

septal recess is in effect a short tube, terminating at the mouth of its equivalent on the preceding septum. Thus successive septal recesses link one septum to the next, forming a tunnel which extends throughout the phragmocone (Pl. 49, fig. 1).

The tunnel is, however, itself septate. A large limb subtended from the median ventral wall of each septal recess, here termed the inner septum, plugs the mouth of the septal recess formed by the previous septum (Pl. 48, figs. 4, 5). In concert the septal recesses and inner septa combine to form an inner phragmocone analogous to the phragmocone proper which surrounds it. Chambers of the two phragmocone systems are linked, a zone of interconnection being provided in the necks of the inner septa which do not close against the mid-ventral sector of the subjacent septal recesses. Text-figure 1 provides a diagrammatic summary of the septal architecture.

The free margin of the septal recess is complexly fluted (Pl. 48, figs. 3, 4). Its third-order subdivisions splay out to form a fringe which reaches beyond the mouth of the previous septal recess, extending across the subjacent planar septal surface to the base of the first-order flutes of the outer perimeter (Pl. 48, fig. 4). Fluting of the inner septum is also complex and represents a smaller scale equivalent to the structure of the outer septal periphery. Margins of the septal recess and inner septum are confluent and comprise the septal lobe of sutural nomenclature (Arkell 1957; Kullmann and Wiedmann 1970). The suture of the inner septum thus comprises a very large median saddle within the septal lobe proper which is formed by the free margin of the septal recess. The septal lobe is confluent with, and may be considered as an extension of, the internal lobe.
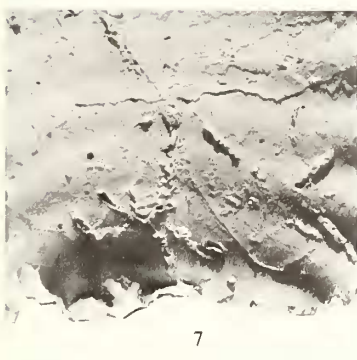
A septal lobe is already present at a shell diameter of 8 mm, the smallest growth stage in the collection displaying a septal surface. Subsequent growth trends are isometric across the size range of septal surfaces available for measurement (text-fig. 2) The pattern of fluting associated with the septal recess and inner septum, like that of the septal periphery, was stabilized early in ontogeny. A detailed comparison of fluting represented at shell diameters of 44 mm and 162 mm shows it to be identical in all respects other than scale. Flutes associated with minor lobes within the septal lobe are more intricately divided and more elongate than those associated with the minor saddles so that the suture shows a marked polarity (Pl. 48, fig. 4).
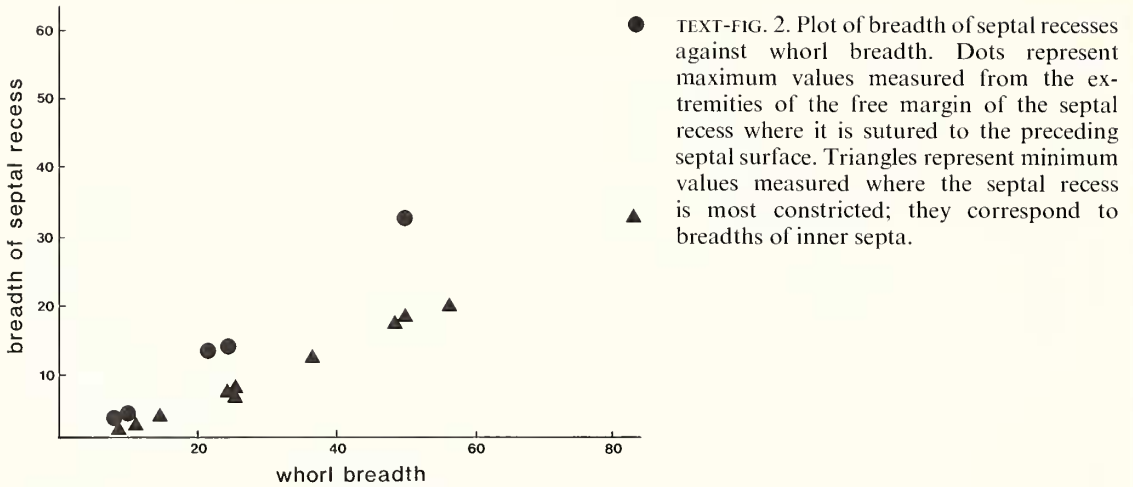
Interpretation

Structures associated with the septal lobe are striking features of *Pseudophyllites* phragmocones and represent a considerable genetic investment in shell architecture and in organization of the posterior

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EXPLANATION OF PLATE 49

Fig. 1. Internal mould of *Pseudophyllites indra* (Forbes) showing two linked septal recesses, one showing the sutural trace of an internal septum. WAM 80.976, × 1·2.

Figs. 2, 3. Two halves of a juvenile shell of *Nautilus pompilius* (Linneus) in which the last septum is incomplete and represented by a rim of shell only. 2, uncoated and showing the mural zones of the two last septa. 3, coated with ammonium chloride and showing that the last septum is widely separated from the mural ridge which bounds the mural zone of the previous septum. OUM 14475, × 2.

Figs. 4–10. Latex peels of internal moulds of ammonites showing structures of the inner shell surface. 4, *Kitchinites* sp. nov. showing midventral ridge on inner shell, NMV P31013, × 3. 5, *Lytoceras cornucopia* (Young and Bird) showing the posterior of the body chamber on the midventral line. Note the ridges extending a short distance into the body chamber and showing an indistinct lobate termination, BMNH 43902, × 3. 6, *Phylloceras heterophyllum* (J. Sowerby), showing midventral ridge with minor ridges converging on to it, OUM J20360, × 3. 7, *Hamites maximus* J. Sowerby showing faint ridges of shell forming a pair of rings straddling the mid-dorsal line of the body chamber immediately anterior to the last septum. Figured by Crick (1898, pl. 17, figs. 6, 7) who regarded them as muscle scars, BMNH C6802, × 3. 8, *Gunnarites kalika* (Stoliczka), showing midventral ridge, WAM 80.845, × 3. 9, *Maorites densicostatus* (Kilian and Reboul), showing midventral ridge, NMV P31023, × 3. 10, *Gaudryceras kayei* (Forbes), showing midventral ridge and subordinate ridges parallel to it, WAM 80.839, × 3.

PLATE 49

TEXT-FIG. 2. Plot of breadth of septal recesses against whorl breadth. Dots represent maximum values measured from the extremities of the free margin of the septal recess where it is sutured to the preceding septal surface. Triangles represent minimum values measured where the septal recess is most constricted; they correspond to breadths of inner septa.

body of the *Pseudophyllites* animal. Their retention as enduring features in the *Tetragonites-Pseudophyllites* stock, and in the Lytoceratina in general, indicates that they served some specific functional role. Given the comparability of fluting associated with the septal lobe with that of the external septal periphery, an integrated function or functions may be adduced for the septal surface *in toto*.

Strength. Since phragmocone strength is the generally accepted functional role attributed to septal design, it is instructive to examine the septal lobe and its associated structures in this context. Fluting related to the septal lobe is entirely internal and therefore cannot have contributed to support of the outer shell. It might be argued that fluting associated with the inner septum contributed strength, and consequent economy in shell thickness, to the median dorsal part of the septal surface *in toto*. As discussed more fully below, each septal surface must, at some stage of phragmocone growth, have carried the hydrostatic load and it has been argued that septal architecture in ammonites reflects a response to this requirement. The internal septum might thus merely represent a somewhat bizarre elaboration of this theme.

However, design of the flared and fluted base of the septal recess intersecting the preceding septal surface at a low angle along a deeply embayed line of suture which displays marked polarity, cannot be readily reconciled with shell strength as its functional role.

Phyletic context. The septal lobe is a structure of considerable phyletic longevity. It is characteristic of the morphologically conservative suborder Lytoceratina whose range extends from early Jurassic to late Cretaceous (Kullmann and Wiedmann 1970). The earliest *Pseudophyllites* are of Santonian age and the genus is best known from the Campanian and Maastrichtian. Origins of the genus are clearly to be found in *Tetragonites* (see Kennedy and Klinger 1977), which also shows a well-developed septal lobe and which first appears in late Aptian times. The septal lobe was therefore a stable morphological feature of the *Tetragonites-Pseudophyllites* stock for some 40 m.y. and was likely to have been stable over a much longer period, probably having appeared in an ancestral lytoceratid stock during the early Jurassic.

The peculiarities of lytoceratid septal architecture cannot be considered as unique among ammonites but, as has long been recognized, merely represent an extreme development of the dorsal flute of the septum corresponding to the internal lobe of the suture. The septal lobe of sutural terminology represents an extension of the internal lobe onto the preceding septum (Wiedmann and Kullmann 1981). Thus the septal recess is homologous with the flute corresponding to the internal lobe which is ubiquitous among ammonites except for a few Devonian forms. The inner septum is

homologous with a minor flute corresponding to a small median saddle contained within the internal lobe of most Mesozoic ammonites.

Organization of associated soft-tissue. Disposition of soft-tissue associated with the formation of each septal recess and associated internal septum is replicated by the shell itself and is complex. The suture line at the free margin of the septal recess marks the intricate termination of a fringe of tissue which followed the shape shown by the distal portion of a septal recess, curving away from the main body of tissue (Pl. 48, fig. 2; text-fig. 3). A space, presumably fluid-filled in life, must have lain between this fringe and the main body of the animal. The inner septum replicates the posterior termination of the animal's soft parts which plugged the narrowest part of the preceding septal recess. Its complex suture represents branching arms of tissue that extended along the walls of the preceding septal recess (Pl. 49, fig. 1).

In moving forward during growth to the site of a new septum, all tissues were withdrawn from the septal recess. To accomplish this, considerable constriction of the fringe would have been necessary as the smallest cross-section of the septal recess is as little as 60% of the area displayed by the associated fringe (Pl. 48, fig. 3; text-figs. 2, 3). The space between the fringe and the main body of tissue would have assisted in accommodating the constriction. The fringe itself must have consisted of tissue with exceptional elastic properties for, having been compressed and distorted, the fringe recovered its original shape, fitting exactly to the mouth of the previously formed septal recess with the fine divisions of its delicately serrated margin reaching across the previously formed septal surface towards its periphery. Collagenous connective tissue organized as a pliant composite, or tissue capable of hydrostatic self-support, would possess the appropriate mechanical attributes (Wainwright *et al.* 1975). Soft tissue lying adjacent to the septal periphery adopted a complex shape of identical type to that of the fringe and was laterally continuous with it. The same type of tissue must therefore have been located along the frilled periphery of the *Pseudophyllites* septum.

The episodic, growth-required stress imposed on the fringe of soft tissue lining the septal recess and producing marked changes in its shape suggests that forward movement of the animal within the shell itself was episodic. It seems likely that short periods of rapid forward movement and distortion of the fringe were followed by long resting periods when the fringe adopted its unstressed shape.

Certain authors (Seilacher 1975; Bayer 1977a) have contended that the posterior of the ammonite animal's soft tissue functioned as a membrane surface prior to septal fabrication. In this model the membranal precursor of the septum is thought to have approximated initially to a planar surface
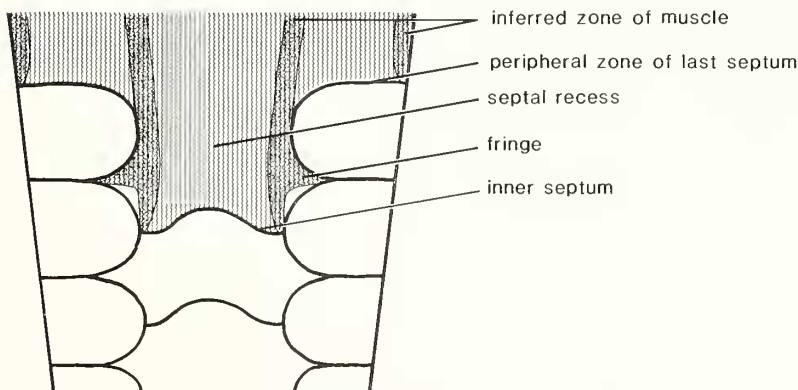
TEXT-FIG. 3. Transverse longitudinal section drawn in the plane of maximum whorl breadth for the last two camerae and posterior body chamber of *Pseudophyllites indra* (Forbes) showing the relationship of tissue to shell.

occupying the whorl cross-section and attached at a number of point locations on its periphery. Hydrostatic or muscular stress acting perpendicular to the initial planar membrane resulted in its deformation and the production of the complex, fluted surface later replicated in shell by secretion of the septum. Deformation was maximized at the periphery of the subsequent septum, with its free segments stretched between the point attachments. Orientation of the major folds in the suture line is thereby controlled by the direction of stress imposed on the membrane.

Fluting of the fringe, of which the free margin of the septal recess is a replica, has a different orientation and cannot have resulted from the same mechanism. Here the sutural folds are orientated perpendicular to the inferred stress direction and are unrelated to it (see Pl. 48, figs. 3, 4).

Fluting shown by the septal recess is identical to, and laterally continuous with, that shown by the outer septal periphery and the inner septum. Furthermore, the entire septal surface was almost certainly the result of a single secretional episode. Clearly the type of tissue, its episodic movement and the secretory processes responsible for formation of the septal recess were general to the entire septal surface.

STRENGTH PARADIGM OF AMMONITE SEPTAL FUNCTION RE-EVALUATED

Accepting that ammonite phragmocones functioned like that of living *Nautilus* and were filled with gas of about one atmospheric pressure which imparted bouyancy to the shell, they may be regarded as sealed vessels required to withstand hydrostatic pressure. Three aspects of phragmocone strength need to be considered: the strength of the outer shell which is supported by the septa, the strength of the septa themselves and the strength of the junctions between the outer shell and the septa on the line of suture. An initial concern, however, is the palaeobathymetry of ammonites and thereby the hydrostatic pressures to which their phragmocones were likely to have been subjected.

Palaeobathymetry

The depth habitat of ammonites is not easily evaluated because shells which are buoyant in life may be easily transported in death to a completely different environment (Reyment 1958). Post-mortem cessation of siphuncular osmotic pumping may have caused flooding of the phragmocone and sinking of the shell to a site of fossilization at much greater depth than that inhabited by the living animal. Alternatively post-mortem separation of body from shell may have caused the latter to float to the surface and drift inshore to a shallow water, even littoral, environment as is common for *Nautilus* (House 1973; Reyment 1973).

The broad palaeoecological context of ammonites is best assessed from the types of sediment in which their remains occur and the nature of fossil assemblages of which they are part. More recent data support the conclusion of Miller and Furnish (1957) that ammonites are predominantly associated with sedimentary rocks of shallow-water origin. McKerrow (1978), in a comprehensive review of British fossil assemblages, many of which are also widely represented in Europe and elsewhere, recorded ammonites as essentially of neritic palaeoecology throughout their history. Casey and Rawson (1973) drew similar environmental conclusions for ammonite-bearing strata of the Jurassic and Cretaceous boreal realm, whilst Kauffman (1977) concluded that the vast epeiric sea which invaded the Western Interior of North America and sponsored an abundance of ammonites had a maximum depth of perhaps 300 m. Cretaceous sediments containing spectacularly diverse ammonite assemblages accumulated in passive continental margin, neritic settings on the borderlands of the Indian Ocean following the fragmentation of eastern Gondwana in Madagascar and southeastern Africa (Blant 1973; Kennedy and Klinger 1975; Basairie and Collignon 1956), Western Australia (Veevers and Johnstone 1974; Henderson and McNamara unpublished) and southern India (Kossmat 1898; Sastri *et al.* 1973).

In comparison, records of ammonites from deep-water sedimentary environments are few. In addition to neritic assemblages, Scott (1940), Ziegler (1967), and Tanabe *et al.* (1978) have recorded distinctive assemblages typified by Phylloceratina and Lytoceratina from deeper water environments

where they were considered to have had benthic or bathypelagic life habits. Phylloceratids and lytoceratids are however best known from shelf sediments and may have been shallow-water nectopelagic organisms whose range extended beyond the continental shelves (Birkelund 1965) and their deep-water associations could well be a post-mortem artefact (Kennedy and Cobban 1976; Tanabe 1979). Ammonites, like all macrofossils, are very rare in Mesozoic eugeosynclinal flysch (continental rise and trench) sediments such as those of the Franciscan assemblage in California (Irwin 1957) and the Torlesse Supergroup in New Zealand (Stevens and Speden 1978) whereas they are much more common in subjacent broadly coeval sedimentary rocks of the northern part of the Great Valley sequence (see also Ojakangas 1968; Matsumoto 1960) and Mirihiku Supergroups respectively where shallower water depositional environments prevailed.

The record of ammonites in deep-sea, pelagic sediments is sparse but its interpretation is rendered equivocal by the dissolution of aragonite shells at depth as shown so clearly by pteropods in the deep-sea Cenozoic record (Kennett 1982). As reviewed by Bernoulli and Jenkyns (1974), Mesozoic ammonite and aptychus-bearing pelagic lithofacies are well known from onshore exposures in the Alpine–Mediterranean region where they are considered to be continental margin deposits which accumulated partly under neritic conditions within the photic zone and partially in deep-water environments. Many of the records of ammonite phragmocones and lamellaptychi from deep-sea drilling and dredging represent neritic deposits of Mesozoic continental margins (Renz *et al.* 1975; Wiedmann and Neugebauer 1978) or deep-water pelagic deposits which are not greatly distant from Mesozoic continental margins (Renz 1972, 1978, 1979*a*, 1979*c*, Wiedmann 1979). However, reports of lamellaptychi from the central Pacific (Renz 1973) and Atlantic sites distant from any continental mass (Renz 1977, 1979*b*) show that some ammonites were fully oceanic. Lamellaptychi are characteristic of the Oppeliidae (Arkell *et al.* 1957), a cosmopolitan family which is well known from shallow-water sediments. All ammonite genera known to occur in deep-sea, pelagic sediments as phragmocones are also known from shallow water occurrences.

Overall the lithofacies and associational data for ammonites support the view of Lehmann (1975) that they were predominantly of neritic palaeoecology and lived in water depths ranging to perhaps 300 m corresponding to a hydrostatic pressure of 30 bars. The contention of Mutvei (1975), based largely on considerations of functional morphology, that ammonites were predominantly denizens of the open oceans where they ranged into deep-water environments, finds no support in the fossil record.

Strength of outer shell

Ammonite phragmocone strength in this context can be assessed in an approximate way by reference to the engineering of thin-walled pressure vessels for which there is a sound theoretical design basis to contend with failure by buckling. As shown by Brownell and Young (1959) the strength of cylindrical vessels subjected to external pressure is governed by the diameter of the cylinder, the thickness of its wall, the spacing of internal strengthening rings or septa, and the elastic properties of the wall material as determined by Young's Modulus. Segments of ammonite phragmocone may be considered as approximations to such vessels. Wall thickness and septal spacing can be measured directly. Young's Modulus has been measured for *Nautilus* nacre (Wainwright *et al.* 1975) and the nacre which comprises the principal shell layer of ammonite phragmocones (Birkelund 1981) may be expected to have shown comparable elasticity. Very few ammonite phragmocones conform to a circular cross-section; a diameter which matches the widest arc of cross-sectional curvature and represents minimum strength seems an appropriate approximation to adopt in the analysis.

Text-figure 4, which is adapted from Brownell and Young (1959, text-fig. 8.4), charts the relationship between cylindrical pressure vessel specifications and strain at failure. By employing Young's Modulus for *Nautilus* nacre, the abscissa may be rescaled for stress. Also shown is the field to which ammonite phragmocones approximate and the stress imposed by a hydrostatic pressure of 50 bars. The strength indicated for ammonite phragmocones assuming planar septa departs from the stress field to which they were probably subjected (up to 30 bars), plus an appropriate safety margin, by an order of magnitude. Whilst it is admitted that the analogy between ammonite phragmocones

pressure in bars
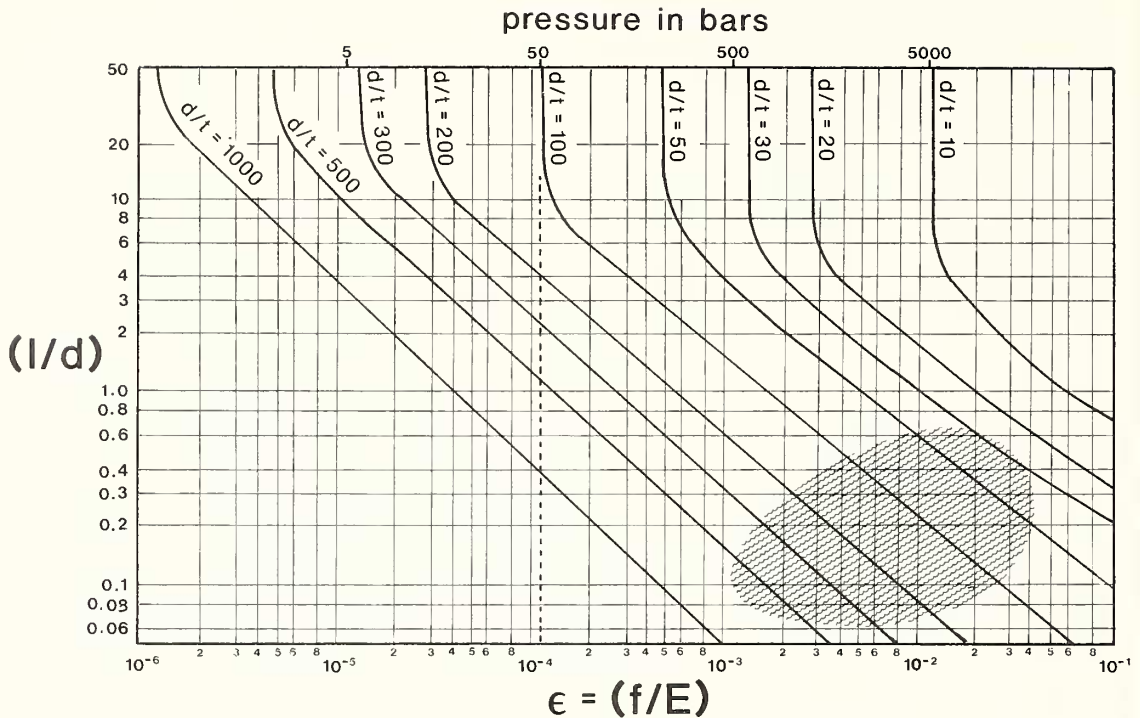
TEXT-FIG. 4. General chart showing relationship between diameter (d), thickness (t), distance between internal septa (1), and strain (e) at the point of failure by buckling for cylindrical thin-walled vessels subjected to external hydrostatic pressure (from Brownell and Young 1959). The field to which Mesozoic ammonites approximate, based on shell measurements for seventy-five taxa, is shaded. A value of Young's Modulus (E), adopted as 44 G Nm^{-2} determined for *Nautilus* nacre by Wainwright *et al*. (1976), allows calculation of a scale in terms of pressure. Even with simple septa, Mesozoic ammonite phragmocones appear to have been immune to failure by buckling at the maximum pressure (50 bars) to which they were probably subjected in life.

and cylindrical pressure vessels is a gross approximation, the disparity between indicated strength and expected stress is so marked that septal fluting, as a design to enhance strength by reducing the effective spacing between septa, seems to be completely unwarranted.

Further, the plan of septal fluting shown by ordinary planispiral phragmocones seems inappropriate if support for the outer shell was the only design consideration. The presence of a convolute internal suture is commonplace in Jurassic and Cretaceous ammonites (sec Wiedmann and Kullman 1981) and represents septal fluting which buttresses directly to the venter of the previous whorl, abutting a shell surface that is already fully supported. The internal lobe straddling the dorsal mid-line is especially noteworthy; it represents a major septal flute in almost all ammonites yet in the vast majority of phragmocones the dorsum is not part of the outer shell and can have carried no hydrostatic load.

There are many ammonites for which fine divisions of the suture, reflecting fine fluting of the septal periphery, cannot have added any appreciable strength to the outer wall. This is true for most ceratitic and pseudoceratitic ammonites in which second-order sutural divisions at the base of the lobes are very fine. The same general argument applies to many Jurassic and Cretaceous ammonites with highly frilled sutures. Often in such forms the finest divisions, or more properly the flutes they represent, contribute little or nothing to minimizing the size of unsupported spans of outer shell. In

addition, the distinctive shape of certain sutural elements is difficult to reconcile with the strength paradigm. A convenient example is provided by the distinctive, phyletically enduring phylloid terminations to saddles of the Phylloceratina.

As shown by Bayer (1977b), the fluctuation in septal distance during growth displayed by several ammonites and the generally poor relationship between the septal spacing and shell form are anomalous in the context of strength. Many authors, most recently Wiedmann and Kullman (1981), have emphasized the conservatism of suture lines, and by implication, septal fluting. Patterns displayed by suture lines often allow stocks of common ancestry to be recognized whereas other aspects of shell morphology, including whorl profile, show wide variation within stocks and repeated convergence between stocks. Given that whorl profile is an important mechanical factor in strength of the outer shell, a close relationship between suture lines and whorl profiles would be predicted by the strength paradigm. Such is patently not the case.

Strength of septum itself

As noted by Raup and Stanley (1971, p. 179) hydrostatic pressure would have affected both the outer shell and the last septum to form part of an evacuated chamber. Body fluids of the living animal would have been at the hydrostatic pressure and the living tissue would have had little strength or at least much greater elasticity than the enclosing shell. At some stage of ontogeny, therefore, each septum would have been obliged to accept the full hydrostatic load. Several authors, for example Westermann (1975) and Wainwright et al. (1976), have noted that the convex form of ammonite septa is generally favourable to withstanding hydrostatic stress.

Septa are too complex to permit any rigorous strength analysis but some general observations are pertinent. The strengths of curved shells is inversely proportional to their radii of curvature and proportional to their thickness. Tensional and compressional strengths of the constructional material are additional factors; for *Nautilus* nacre compressional strength is approximately twice that of the tensional strength (Wainwright et al. 1976) and a similar contrast may be expected for the nacre of which ammonite septa are constructed. To conform to the strength paradigm, each subzone of a septum should be of equal strength. Since shell thickness does not vary between convex flutes and concave flutes, though these would have experienced compressional stress and tensional stress respectively, the two types of flute should show marked differences in radii of curvature. However, suture lines show that this is not the case; in almost all ammonites lobes and saddles are invariably of comparable widths.

Proliferation of fluting towards the septal periphery resulted in shell economy, reduction in radii of curvature of the flutes being reciprocated by a reduction in septal thickness. Enhancement of the weight/strength relationship, however, was not required to maintain buoyancy. Calculations by Mutvei and Reyment (1973) and Heptonstall (1970) have shown that ammonite phragmocones possessed a buoyancy potential beyond the requirements of the living animal, so much so that several chambers must have remained flooded.

Shell economy would have been desirable from a metabolic standpoint. If proliferation of fluting represented such a strategy, then it was not fully exploited. As well known to ammonite specialists, even slight abrasion of phragmocone moulds or steinkerns results in a considerable reduction in sutural complexity. In other words, fine-scale fluting is restricted to a very narrow zone at the periphery of septa. Radial lengthening of fine-scale flutes into a broader zone would seem desirable if shell economy was a matter of vital concern.

Strength of suture

Pfaff (1911) considered the suture between the septum and the outer shell to have been a zone of structural weakness and that linear elongation of the suture imparted necessary strength to the junction. He cited as evidence the allometric relationship between septal diameter and length of suture which he regarded as typical of ammonites. Since septal area, and therefore total hydrostatic load, increases in proportion to the square of its diameter whereas the circumference increases in

linear proportion to the diameter, such a relationship may be interpreted as necessary to maintain sutural strength.

However, shear strength of the interface between septal nacre and the interior surface of the outer shell at the line of suture has never been mechanically evaluated and there is no *a priori* reason for assuming it to be a zone of special weakness. Further, as noted by Westermann (1975) if the junction was a zone of mechanical weakness the septum could be wedged out against the outer shell over a broad zone of contact. This would seem a more expedient solution to the problem rather than maximizing the length of contact by sutural frilling.

Conclusion

It would be in error wholly to deny the strength as a consideration in the design of ammonite septa; clearly there are several aspects of septal morphology that are consistent with such a function. Equally, it is evident that strength is not the only, nor probably the major, consideration. Septal elaboration in ammonites generally, as in *Pseudophyllites* and lytoceratids of similar shell architecture, must have served some other function.

MUSCLE ATTACHMENT PARADIGM OF SEPTAL FUNCTION

The idea that fluted margins of septa may have assisted in attaching the body of an ammonite to its shell was first noted last century and reintroduced by Spath (1919). It has subsequently been listed among alternatives for septal function in a number of reviews (for example, Raup and Stanley 1971; Westermann 1971; Kennedy and Cobban 1976) but the case has never been argued in detail.

Accepting that the attachment of body to shell in the Mollusca is intimately related to muscle attachment, it is instructive to consider the interface between muscle and shell. The general mechanism which applies in molluscs has been described by Hubendick (1957) with important emendations from Nakahara and Bevelander (1970) and Tompa and Watabe (1976). The muscle base is attached to a layer of specialized mantle epithelium, the tendon layer, from which extracellular fibres extend into the adjacent shell surface. Organic extensions from the living tissue are thereby physically embedded in the shell. During growth-required translocation of muscle attachment it is thought that mantle cells adjacent to the leading edge of the muscle base become transformed into tendon cells and extend the tendon layer. New muscle tissue is added above the tendon layer addition and concomitantly part of the tendon layer and associated muscle is atrophied at the trailing edge of the muscle base. In this way muscle bases track across pre-existing mantle in steady, progressive movement as documented for the oyster *Crassostrea* by Galtsoff (1964).

However, this mechanism cannot apply to ectocochleates in which the shell is much larger than the body. Here the entire mantle must move forward in the shell during growth because the shell is growing much faster than the body. The style of growth is more like an ecdysis with older portions of the shell progressively evacuated by the body rather than the steady, matched growth of body, mantle, and enclosing shell seen in most molluscs (text-fig. 5). It follows that muscle attachment cannot have been permanent with extracellular extensions embedded in the adjacent shell. If this were the case the mantle would have been rendered immobile, always pinned to the shell at the zone of muscle attachment. Rather, a temporary means of attachment must have applied, allowing the tendon layer to detach from the shell, move forward to a new site, and reattach. This type of muscle translocation is unique to ectocochleate cephalopods and is unstudied. Perhaps a cement, similar to that demonstrated by Bonar (1978) for muscle attachment of the nudibranch *Phestilla* to its larval shell and destroyed during metamophosis to a shell-less adult, provided the attachment mechanism. The presence of a thin 'chitinous' layer covering the shell on areas of muscle insertion (Griffin 1900) supports this view. However, the ease with which dead *Nautilus* are slipped from their shells suggests an organic means of attachment, maintained by living tissue, was also involved.
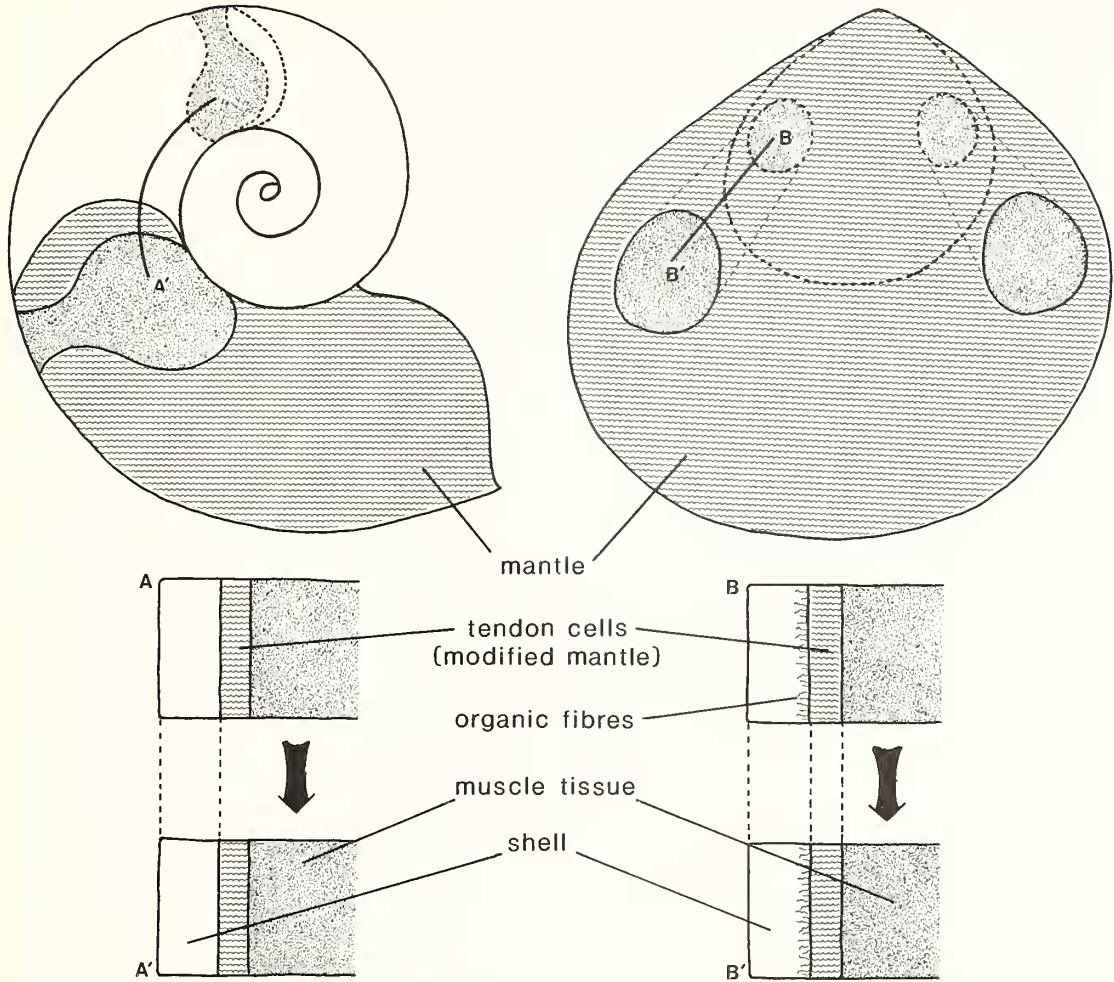
TEXT-FIG. 5. Diagram contrasting mechanisms of muscle translocation shown by ectocochleate cephalopods, typified by *Nautilus*, and most other molluscs, typified by a bivalve. In *Nautilus* the shell is much larger than the body and enveloping mantle which must be moved forward in the shell, complementary with muscle translocation during growth. In the bivalve, mantle underlying the muscle bases is permanently bonded to the shell by extracellular organic fibres. Muscle translocation is achieved by growing new muscle tissue over pre-existing mantle at the advancing edge of the muscle base and complimentary wasting of muscle tissue at the trailing edge.

Proposal for muscle attachment in Pseudophyllites indra

The suture of *Pseudophyllites* is complex to the degree where its convolutions occupy all the available surface area of the outer shell save for a narrow zone adjacent to the mid-ventral line where the sides of the vental lobe do not quite meet (text-fig. 6a). Fine-scale fluting of the septa had reached its ultimate expression and was so from the early stages of shell growth as sutures are fully differentiated at shell diameters as small as 2 cm. Development of the septal recess and inner septum might be regarded as morphological strategies designed to extend the free septal margin and fine-scale fluting associated with it.

a   b   c
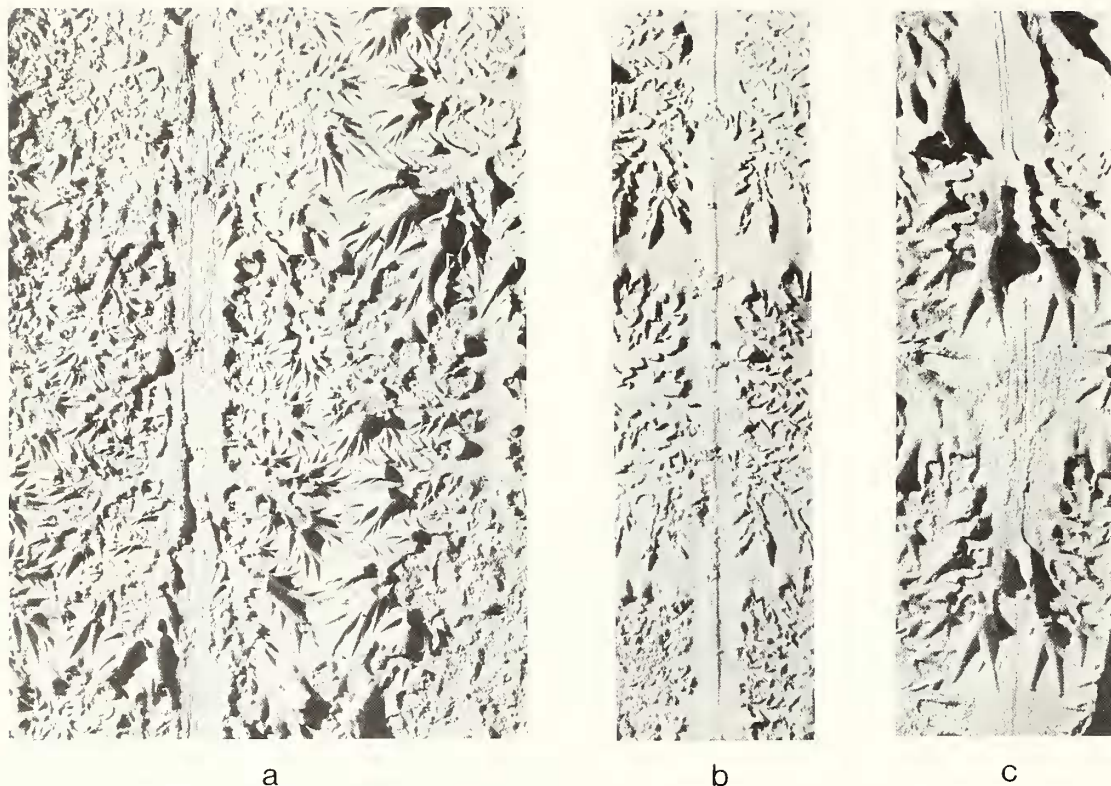
TEXT-FIG. 6. Latex casts taken from natural internal moulds of ammonite phragmocones to show details of the inner shell surface. *a*, *Pseudophyllites indra* (Forbes) showing fine-scale ridges and grooves along the ventral midline and the intricate fluting of the septal periphery; WAM 60.130, × 2. *b*, *Pachydiscus* sp. showing a broad median ventral ridge; WAM 81.2693, × 3. *c*, *Phylloceras* (*Neophylloceras*) *meridianum* Spath showing narrow median ventral ridge with indistinct ridges and grooves lateral to it; holotype BM(NH) C41320, × 2.

As already discussed, inferences concerning the fringe of soft tissue associated with the septal recess in life suggest it was resilient in nature, capable of accepting stress by distortion followed by elastic recovery to its original shape. If the tissue possessed any appreciable strength, as might be expected from its elastic properties, it must have acted to hold the animal in its shell. A similar case can be argued for the tissue once associated with the fluted vaults lying beneath the outer shell at the septal periphery and at the margin of the inner septum. Fluted terminations of the vaults are widely splayed so that soft tissue contained in them must have been deformed when drawn forth during growth (Pl. 48, fig. 3; text-fig. 3). Accepting that attachment of body to shell is typically associated with the musculature in molluscs, it may be that the fine-scale flutes represent sites of muscle attachment.

Soft-part organization in ammonites is very poorly known and the nature of musculation can only be surmised from analogy with extant *Nautilus*. Mutvei (1957) has reviewed *Nautilus* musculature which is inserted on the annular elevation, a broad zone on the inner wall of the shell immediately in front of the last septum. Three distinct zones of muscle insertion are represented: the subepithelial muscle which originates from a narrow band at the posterior edge of the annular elevation and abutting the last septum; retractor muscles which originate from the lateral sectors of the annular

elevation and contribute the bulk of the muscle attachment area; and the mantle musculature which originates from a narrow band at the anterior margin of the annular elevation. Although insertion of the retractor muscles is lateral, the muscles themselves lie in the dorsal part of the viscera each having a reniform cross section and terminating in the cephalic cartilage (see Mutvei 1964b, text-fig. 2; Kennedy and Cobban 1976, text-fig. 5).

If the free septal margins represented the location of muscle attachment in *Pseudophyllites*, two subzones are apparent. The free margin of the septal recess and periphery of the inner septum would have contributed a pair of muscles located dorsally in the visceral mass and each with a reniform cross-section. The septal periphery would have contributed a sheet of muscle to the outer body wall. Such a system of musculature is strikingly similar to that displayed by *Nautilus*, the paired muscles representing retractors and the peripheral muscular sheet representing the mantle and subepithelial muscles.

The process by which the muscle attachment sites are translocated in *Nautilus* prior to the accretion of a new septum is poorly understood. Fine growth-lines on the retractor muscle scars show that these muscles were moved forward along the wall of the body chamber in very small increments, each one marked at the leading edge by a minute rim of prismatic myostracum. X-ray radiography by Ward *et al.* (1981) has shown that movement of the animal forward in its shell is episodic and rapid, taking place in less than 6 days in a cycle of chamber formation of over 70 days. In contrast, shell growth at the aperture proceeds at a slow and constant rate.

Growth-required movement of the *Pseudophyllites* animal is also thought to have been rapid because it necessitated distortion of the soft-tissue at the posterior margin of the visceral mass. Disposition of tissue responsible for secreting the septal recess (text-fig. 3) may be cited in evidence; with initiation of forward movement of the animal in its shell the fringe must have suffered distortion in shape, increasingly so as it was drawn past the central constriction of the septal recess. It would not have recovered its original shape until the forward movement had stopped. Tissue filling the fluted vaults at the septal periphery would have experienced a similar pattern of distortion and recovery.

It is suggested that muscle translocation was accomplished in a more dramatic way in *Pseudophyllites* where the muscles were inserted on the septal periphery, compared to *Nautilus* where the muscles are inserted on the wall of the body chamber. At the onset of movement, the muscles detached completely and were refastened to a newly accreted septum at the cessation of movement. This scenario suggests very rapid movement, perhaps only of a few hours, when body functions dependent on longitudinal musculature would have been suspended.

Septal surface periphery as a template for muscle organization

Accepting a need for temporary muscle attachment on the septum of a tubular, subepithelial muscle sheet as general for ammonites, the complex fluting at the septal periphery may be seen as a strategy for increasing the surface area of muscle attachment. This may have been required simply for bonding muscle to shell or, alternatively, as facilitating rapid secretion of the septal periphery prior to muscle insertion. The pattern of suture can therefore be regarded as expressing organization of the musculature; its complexity and diversity among ammonites reflects evolution of the longitudinal muscle system.

Fluting associated with major sutural lobes in Mesozoic ammonites is invariably dendritic in form with larger flutes subdividing to smaller ones; in taxa with complex sutures, four orders of fluting are represented on the septa. Muscle fibres within the fine-scale flutes, and inserted near their junction with the outer shell, would thereby have been aggregated in dendritic fashion forming thick bands of muscle tissue extending forward from the major lobes with thinner bands of muscle tissue extending from the major saddles where the dendritic pattern is less well developed (text-fig. 7). Seen in this way, unusual shapes of saddle termination, characteristic of Phylloceratina and various stocks of pseudoceratitic ammonites find a ready explanation. They are merely by-products of the particular dendritic form adopted by the lobes. The progressive, overall elaboration of sutures, from goniatitic to ammonitic grade, may be considered as complementing a general advance in organization of the
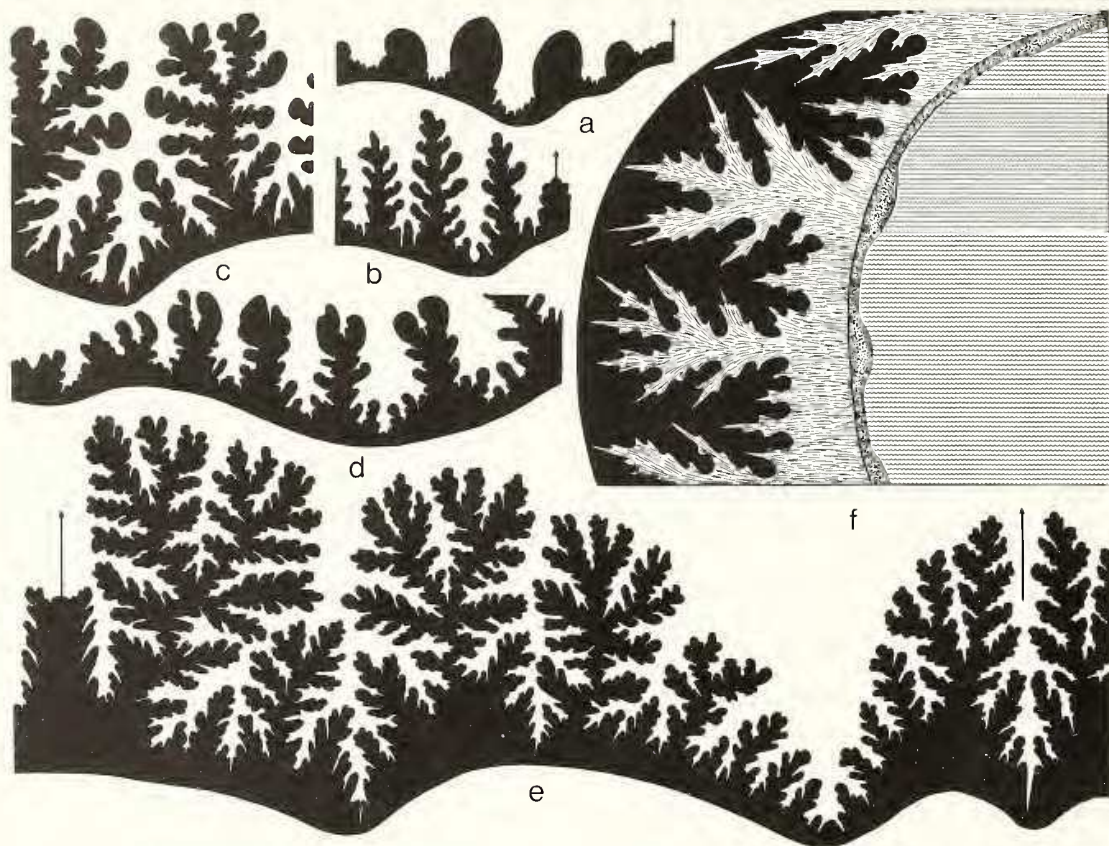
TEXT-FIG. 7. *a–e*, typical Mesozoic ammonite suture lines illustrating their dendritic nature, all × 1. Ceratitina: *a*, *Hedenstroemia hedenstroemi* (Keyserling) (redrawn from Spath 1934); *b*, *Psilosturia mongolica* (Diener) (redrawn from Diener 1895). Phylloceratina: *c*, *Phylloceras* (*Hypophylloceras*) *onoense* (Stanton) (redrawn from Matsumoto 1959). Ammonitina: *d*, *Hypengonoceras warthi* (Kossmat) (redrawn from Kossmat 1895); *e*, *Puzosia planulata* (Sowerby) (redrawn from Kossmat 1898). *f*. hypothetical reconstruction of body wall in relation to the last septum. Longitudinal muscle fibres originate at the margin of the septum resulting in a continuous muscular sheath which thickens adjacent to lobes of the suture where investment in muscle attachment is greatest.

musculature. The appearance of fine subdivisions of the primary lobes in sutures of the intermediate ceratitic grade is readily explained as part of this trend.

If the septal recess and inner septum anchored the retractor muscle in the Lytoceratina then its morphological equivalent in other suborders, the internal lobe, would also have served this function. The investment in retractor musculature in ammonites other than the Lytoceratina would seemingly have been very limited and the musculature would have comprised little more than a subepithelial sheet enveloping the body. Body-chamber shape suggests that many ammonites had elongate, worm-like bodies (Mutvei and Reyment 1973; Kennedy and Cobban 1976) curved through more than one volution of the shell in some forms. In the heteromorphs the body was often elongate and was required to adopt different shapes as determined by changes in shell coiling that occurred during ontogeny. Body shape in all such forms is compatible with a tubular muscle sheath, less so with a pair of powerful retractors. For retractors to be efficient, their curvature needs to be limited, as in *Nautilus*

(see Mutvei 1964b; Kennedy and Cobban 1976). It might therefore be expected that the Lytoceratina should display short bodies accommodated in inflated, rapidly expanding shells of evolute form, as indeed is typical of the group (see Arkell *et al.* 1957).

It is of interest to note that shell fluting in response to organization of the musculature was independently developed, in an incipient way, by members of the 'nautiloid' orders Oncoceratoida and Discoceratoida during Ordovician time. In these groups the annular zone of muscle insertion at the base of the body chamber is ornamented with short ridges and intervening hollows. A larger paired muscle platform, thought to have been the site of retractor insertion, lies on the midline and is generally regarded as ventral (Sweet 1959; Teichert 1964). On some shells the ridges buttress the septum (text-fig. 8) and although they originate from the shell wall, they may be likened to the small septal flutes which buttress the shell wall in ammonites of the Triassic family Sageceratidae or the Cretaceous family Sphenodiscidae.

a   b
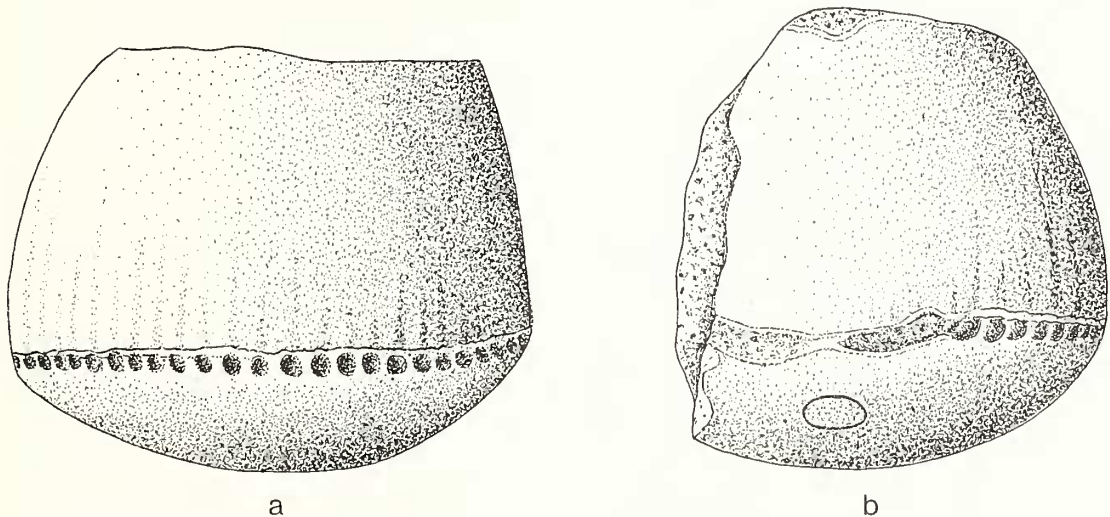
TEXT-FIG. 8. Internal mould of the Upper Ordovician Oncoceratid nautiloid *Diestoceras* sp. drawn from Sweet 1959, p. 42, figs. 6, 7. *a*, lateral view. *b*, ventral view; × 1. The muscle attachment zone (annulus) lies on the posterior surface of the body chamber immediately adapertural of the last septum and carries nodes which increased the surface area for muscle attachment.

Shell structure in Sciponoceras

If the septal periphery represents a zone of muscle insertion, it should carry prismatic shell which is the characteristic myostracum of molluscs. The septal periphery, because of its convoluted nature, is often difficult to examine for micro-fabrics. Juvenile *S. glaessneri* Wright from Bathurst Island, northern Australia are ideal for this purpose, displaying both simple sutures and empty phragmo-cones in which the original shell fabrics are perfectly preserved. As shown in text-figure 9 the junction between septum and shell wall is complex. A band of prismatic shell, here termed the preseptal prismatic zone, precedes the septum and is clearly distinct from the inner prismatic layer of the shell wall. It is narrow and sharply defined in the saddles, becoming broader and more diffuse in the lobes (text-fig. 9a). A second layer, of nacre, comprises the septum proper and wedges out against the inner prismatic layer of the shell wall (text-fig. 9c). A third band of shell with prismatic microstructure and

here termed the post-septal prismatic zone lies on the apron of the septal nacreous layer lapping on to the adjacent inner prismatic layer of the shell wall (text-fig 9*b*, *c*). In the saddles, where the angle between septum and outer shell is obtuse, its development is unconstrained and it forms a ridge. In the lobes, however, it lies in an acute angle between septum and outer wall and no such ridge is developed.

The postseptal prismatic zone of *S. glaessneri* is regarded as the location of subepithelial muscle insertion. Related structures have been identified in a number of studies of ammonite shell microstructure. Howarth (1975) observed that septal nacre in the Dactylioceratidae is replaced by prismatic shell, thickened to form a ridge, at the junction of septum and outer shell. According to Kuliki (1979, pl. 44, fig. 2), a similar transition marks the margin of septa in *Quenstedtoceras*. Birkelund and Hansen (1974, 1975) described a prismatic layer on the adapertural face of septa in *Hypophylloceras*. It appears to thicken at the septal periphery (Birkelund and Hansen 1974, pl. 9, fig. 2) gradually replacing nacre at the confluence of septum with shell wall (Birkelund and Hansen 1975, pl. 1). Well-preserved internal moulds of Cretaceous ammonites often show a faint gutter immediately adapertural of each septum in the crests of saddles (text-fig. 9*d*; see also Kennedy and Cobban 1976, pl. 2, fig. 3*a*). The gutter reflects a ridge of shell similar to that of *S. glaessneri* and probably represents the postseptal prismatic zone.

The preseptal prismatic zone is represented in *Nautilus* as a ridge of shell lying in the angle each septum makes with the shell wall. Mutvei (1964*a*) recorded it as the supraseptal ridge but, as his interpretation of ectocochleate orientation has not been widely accepted, this term is not used here. In addition to *Nautilus*, Blind (1975, 1976, 1980) recognized it in some Palaeozoic nautiloids and in a few taxa of ammonites. According to Blind, the preseptal prismatic layer corresponds to the mural ridge, an annular band of prismatic shell deposited as myostracum to a band of subepithelial muscle attachment which abuts the adapertural edge of the septum where it finally wedges out against the shell wall. Blind supposed that the mural ridge served a double function: first, as a zone of muscle attachment and secondly as a precursor elevation of shell to which the posterior of the animal's body is fitted prior to the secretion of a new septum. This suggestion was also adopted by Ward *et al.* (1981) who documented chamber formation in living *Nautilus* by X-ray radiography.

Contrary to these views, however, the preseptal prismatic zone and the mural ridge of *Nautilus* are quite separate, unrelated structures (Pl. 49, figs. 2, 3). The preseptal prismatic zone is here considered to represent an immediate precursor to secretion of the septum proper. It is thought that when the animal had moved forward to the position of a new septum, the band of myoadhesive epithelium at the posterior margin of its body established adhesion by secreting the preseptal prismatic zone. With the body thus stabilized in position, a new septum was secreted beginning at the periphery as reported by Willey (1902, p. 749).

The preseptal prismatic zone of *Sciponoceras* is thought to have served a similar role. A portion of the myoadhesive epithelium at the perimeter of the posterior, septa-forming part of the mantle adhered to the shell wall and secreted prismatic shell. The nacreous layer of the septum proper was then rapidly added, followed by a second zone of prismatic shell, the preseptal zone, which marked the stable location of muscle insertion until such time as a new septum needed to be formed.

Shell wall markings interpreted as muscle scars

If the septal periphery is to be regarded as the principal site of muscle attachment, consideration must be given to various markings on internal moulds of ammonite body chambers that have been interpreted as muscle scar impressions by a number of workers (see Kennedy and Cobban 1976, p. 10).

The best-known structures consist of two narrow gutters enclosing a pair of matched shapes on the mould, symmetrically disposed on its dorsal surface. In planispiral ammonites each gutter encloses a semi-elliptical area abutting the last septum whereas in the heteromorphs each gutter typically forms a ring, completely enclosing an oval or bean-shaped area which lies some distance in front of the last septum (Pl. 49, fig. 7). The areas so defined have generally been interpreted as the sites of retractor muscle insertion, comparable to those of *Nautilus* (Kennedy and Cobban 1976). In *Nautilus* the retractor scars are bounded adaperturely by an annular ridge of shell to which subepithelial muscles
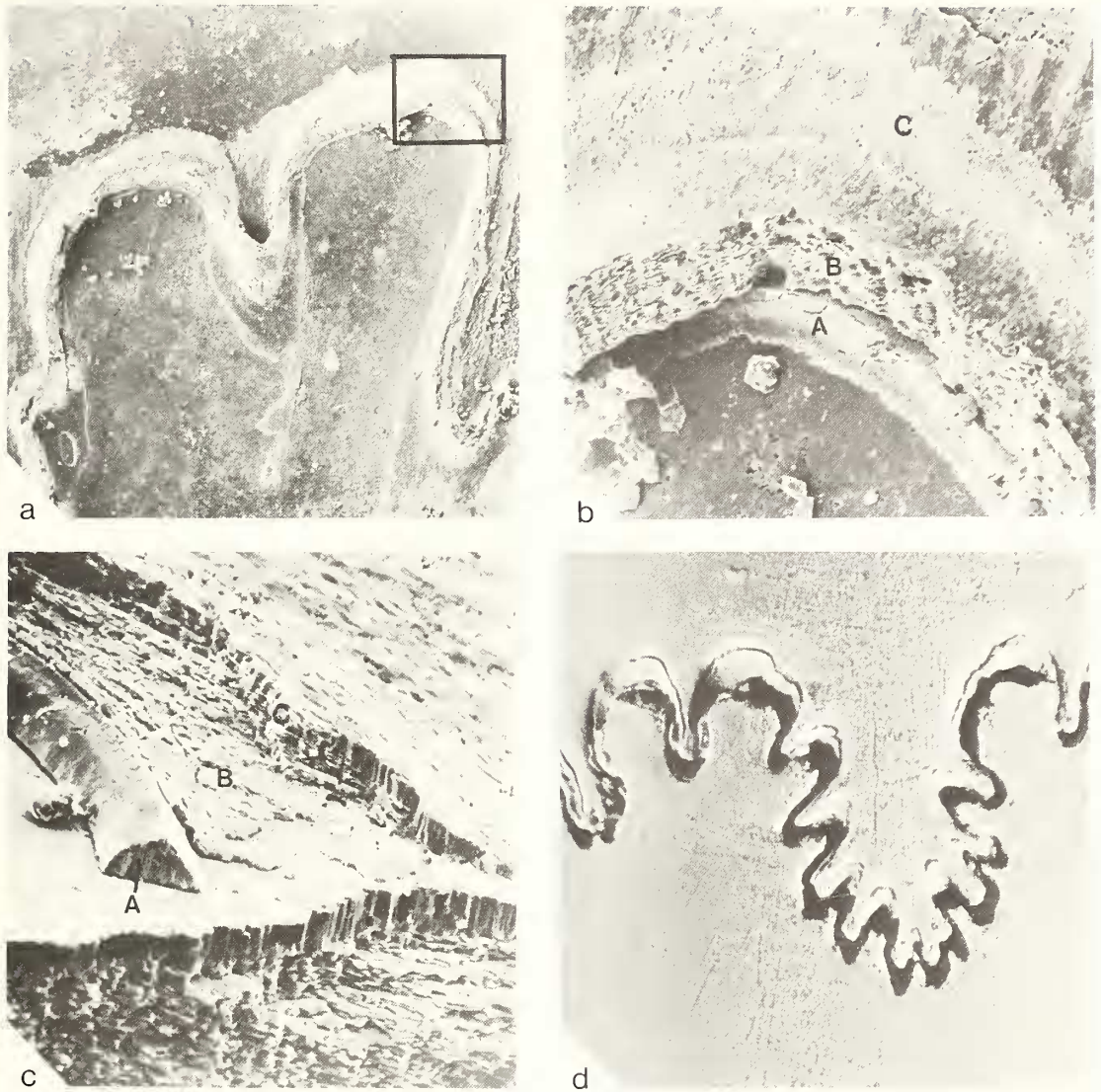
TEXT-FIG. 9. *a–c*, microstructure at the septal periphery of juvenile *Sciponoceras glaessneri* Wright. *a*, plan view of septal junction with outer shell adjacent to a saddle of the suture; × 30. *b*, detail of (*a*) as indicated showing the preseptal prismatic zone (A), the nacreous septal periphery (B) and the post-septal prismatic zone (C); × 180. *c*, broken shell surface in the saddle of a suture showing the shell wall (thin inner prismatic layer and thick nacreous layer), the preseptal prismatic layer (A), the nacreous septal periphery (B) and the postseptal prismatic zone (C); note the superpositional relationships of the preseptal zone, septum proper and postseptal zone; × 225. *d*, dorsal lobe of *Baculites ovatus* Say on an internal mould showing a well-developed gutter immediately adapertural of the suture proper, interpreted as a mould of the postseptal prismatic zone.

were attached (Mutvei 1957). The gutter on ammonite body chamber moulds, or rather the ridge of shell it replicated, is not homologous with the annular ridge of *Nautilus*. As clearly shown by the heteromorphs, in which it forms a complete ring, it cannot represent the site of subepithelial muscle insertion. The retractor scars in *Nautilus* carry a layer of prismatic myostracum and are clearly marked by growth lines, neither of which have been identified on their supposed counterparts in ammonites. Perhaps the markings represent the imprint of internal organs which pressed against the mantle and had their outlines recorded on the shell.

A variety of other structures have been described from internal moulds as representing zones of muscle attachment on the outer shell, most recently by Jordan (1968). They include lobate markings lying immediately adapertural to the ventral saddle of the last suture (sometimes showing as a continuous track along the siphuncular line), large tongue-shaped markings on the flanks of body chambers, and annular markings encircling the posterior of the body chamber. They are much less common than the paired dorsal structures and are commonly defined by staining or by slight differences in texture of mould surfaces. Their interpretation is considered here to be conjectural. Some of the ventral structures may record growth of the siphuncle according to the proposals outlined below.

It should be noted that acceptance of such structures as muscle scars does not wholly invalidate the model of septal muscle attachment argued here. They could be viewed as additional sites of muscle attachment, separate from those of the subepithelial sheath.

Growth model for siphuncle

The model of septal muscle insertion, in which the animal episodically detached its muscles and moved rapidly forward in its shell to a new site of septal fabrication and muscle insertion, has implications for the siphuncle. New siphuncle could not have grown at such a rapid rate and a length of siphuncle, sufficient for the increment of forward movement, would need to have been performed. This problem does not apply to *Nautilus* where forward movement of the body, although episodic, is thought to take several days (Ward *et al.* 1981).

Only the hard sheath of ammonite siphuncles is preserved, consisting of connecting rings (horny organic tissue perhaps mineralized in some taxa) and calcareous funnels at the ventral margins of septa formed by an extension of the septal nacre (septal necks) or by independent structural elements (false septal necks and auxiliary deposits). The disposition of these various elements shows considerable variety among different ammonite stocks (Birkelund 1981).

Any proposal for the growth of the siphuncle and fabrication of its protective coating must account for the following features shown by the sheath and the midventral line of the inner shell wall:

1. The range of geometries and relationships of its structural components.

2. Location of the connecting rings on the ventral midline in contact with the shell wall. In some taxa the septal necks are also in contact with the shell wall but in many others they lie free.

3. The prochoanitic projection of septal necks.

4. Projection of the connecting rings into the living chamber in some phylloceratid taxa as reported by Drushchits and Doguzhayeva (1974), Kuliki (1979), and Westermann (1982).


TEXT-FIG. 10. Morphology of the siphuncular sheath and tissue inferred to have been responsible for its formation. *a–c*, inferred disposition of tissue at the posteroventral margin of the ammonite animal. *a*, soft parts adjacent to the tip of the ventral saddle of the last septum showing the siphuncle and the parting in the mantle above the siphuncle. *b* and *c*, cross-section and longitudinal section of (*a*) showing invagination of the mantle to form a sleeve. *d, e*, diagrams showing components of the siphuncular sheath comprising septal necks (dashed) connecting rings (black) and false septal necks and auxiliary deposits (blank); adapted from Birkelund (1981) and orientated with the adapertural portions uppermost. *d, Saghalinites. e, Tetragonites. f, Phylloceras (Hypophylloceras). g, h*, decoupling of mantle sleeve and secretion of hard parts as the ammonite animal moves forward in its shell during growth, shown in longitudinal section. Mantle of the sleeve secretes the septal neck while mantle of the siphuncle itself secretes the connecting ring.
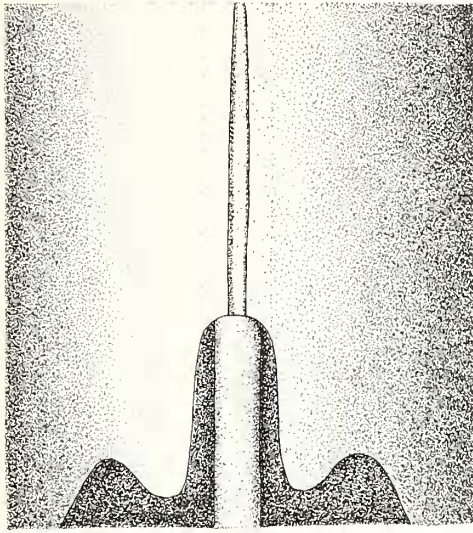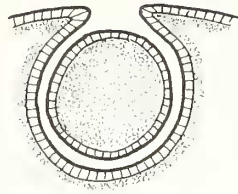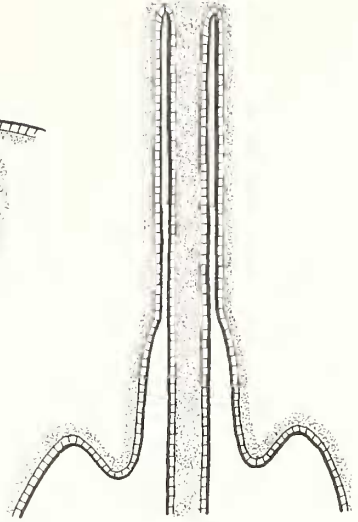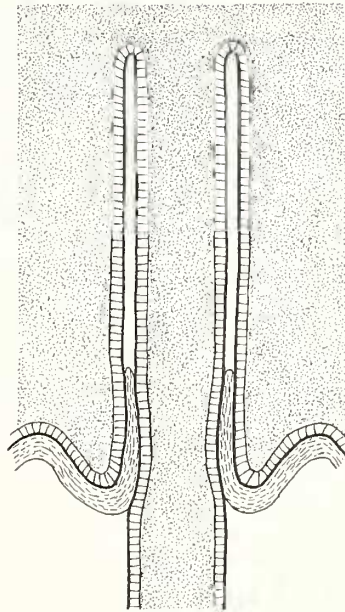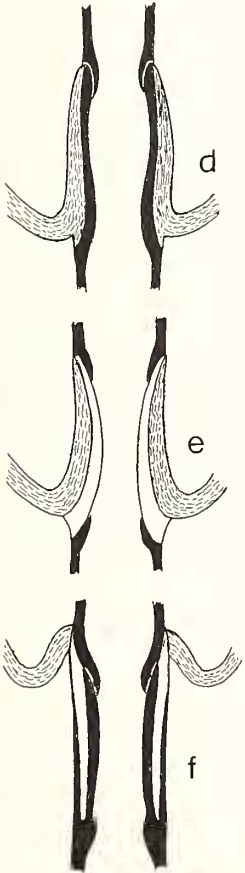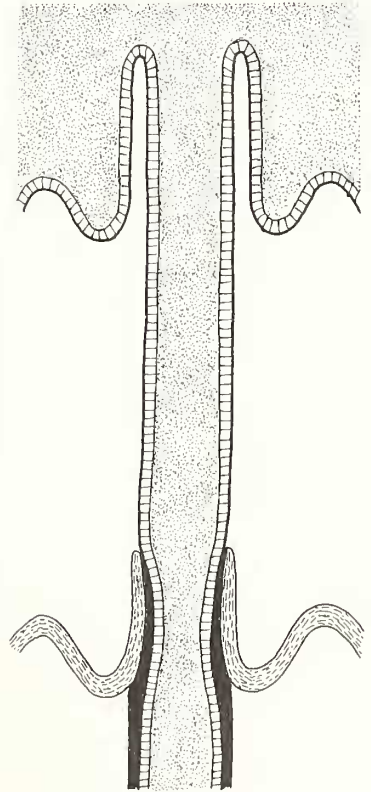
5. The existence of horny membranes which connect the siphuncular sheath to the shell wall and to the septa in a variety of taxa (Grandjean 1910; Westermann 1971; Erben and Reid 1971; Kuliki 1979).

6. The presence of fine longitudinal grooves and ridges which show on the inner shell surface along the midventral line on many phragmocones and is doubtless related to the formation of the siphuncle (Pl. 49, figs. 3–5, 7–9, text-fig. 7). On other phragmocones this zone of the inner shell is smooth.

Given such specifications, the mode of growth of the siphuncle is severely constrained. A siphuncular growth model involving the preformation necessary for rapid forward movement of the animal proposed here is consistent with the observed morphology of the sheath. It is thought that the siphuncular mantle extended along the ventral midline at the posterior of the body and invaginated itself to form an outer sleeve which opened along the midline as a slit (text-fig. 10). At its posterior margin, the sleeve was continuous with the septal-secreting part of the mantle. Growth of the siphuncle and its sleeve is envisaged to have been slow and constant with their zone of formation migrating forward with respect to the remainder of the body. Prior to forward advance of the body at the initiation of an episode of chamber formation, the new length of preformed siphuncle was detached from the outer sleeve via the slit and adpressed to the shell wall by contraction of the musculature of the body wall. In some taxa, horny membranes that accreted on the mantle of the sleeve braced the siphuncle to the shell wall and to adjacent parts of the septum (Kuliki 1979; Birkelund 1981). They have been most commonly described from close proximity to septa in those taxa where the septal neck is not in contact with the shell wall and a small part of the adjacent connecting ring is suspended within the chamber. A more general means of attachment of the siphuncle was provided when its mantle began secreting the connecting ring, thereby cementing it to the shell wall. The midventral markings on the inner shell wall represent shell secretion at the lip of the slit in the sleeve. A median ridge is its common expression (Pl. 49, figs. 4–6, 8–10; text-fig. 6b, c) and the adjacent set of fine markings may represent shell secretion by folds in the mantle which formed as tissue near the slit was compressed by enlargement of the siphuncle beneath. The faint lobate markings lying on the midventral line and some distance in front of a septum (Pl. 49, fig. 3) which shows on rare specimens may mark the zone where the siphuncular mantle invaginated to form the sleeve rather than a site of muscle insertion as some authors would have it.

Secretion of a new septum followed movement of the body, slipping past the newly emplaced segment of siphuncle (text-fig. 10g, h). The posterior part of the siphuncular sleeve secreted the septal neck which was structurally continuous with the septum. False septal necks and auxiliary deposits (text-fig. 10e, f) are considered to be mineralized parts of the connecting ring proximal to the new septum and to have been secreted by the mantle of the siphuncle rather than that of the sleeve. The connecting ring inclusive of its mineralized parts is invariably constricted in the septal neck (text-fig. 10d–f) indicating that the final part of each segment of connecting ring formed later than the septal neck to which it relates. The segmented nature of the connecting ring, with individual segments joined together within the septal neck or at its termination (text-fig. 10d–f), show that its secretion was episodic, with a hiatus following the completion of each new septum.

Mesozoic ammonites show marked changes in siphuncular organization during growth. Very early growth stages commonly display a morphology like that of *Nautilus*, with retrochoanitic septal necks and connecting rings suspended free within the chambers (Spath 1950; Kuliki 1979). The siphuncular organization of adults proposed here could easily have been developed from such a precursor by gradually moving the position of the siphuncle and by progressively developing an evagination of its mantle.

Shell shape and ornament

The type of growth experienced by the ectocochleate animal influences the gross nature of its shell. In nautiloids the body movement is gradual and the muscle insertions track across the inner shell wall. Here the body can expand its girth by gradual growth to fit a shell form in which there is a rapid increase in expansion rate. Ornate shells with corrugated inner shell surfaces are not conducive to the translocation of muscles by this mechanism.

The converse is held to be true for ammonites. Here the animal moves rapidly forward in the shell and is therefore required to expand its girth rapidly to fit the new whorl dimensions. It might be expected that ammonite shells should generally show more gradual whorl expansion rates than nautiloids. A comparison of shell shape in Mesozoic ammonites and nautiloids provided by Ward (1980) shows that this is indeed the case. Transposition of the ammonite body would have been unconstrained by irregularities in the shell wall because muscle tracking was not involved. The striking contrast between Mesozoic ammonites and nautiloids in the general development of ornament thereby finds a ready explanation.

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